

# DECAPODS IN AMMONITE SHELLS: EXAMPLES OF INQUILINISM FROM THE JURASSIC OF ENGLAND AND GERMANY

by R. FRAAYE and M. JÄGER

**ABSTRACT.** Inquilinism is that association in which one organism lives within another, using the host as a place of refuge. Four specimens are described from the Jurassic of England and Germany which illustrates ammonite inquilinism by decapods. The inquiline use of ammonite shells in the geological record, and its ecological and taphonomical implications are discussed.

LOBSTERS are heavily armoured decapod crustaceans that generally inhabit holes and crevices of marine rocky and coralline environments. During Mesozoic times ammonites not only provided a food source for decapod crustaceans and other benthic organisms, they were also perfect places of shelter on otherwise fine-grained sea floors. Several fossil groups have been found preserved inside ammonite body chambers. This mode of preservation is referred to as *inquilinism*, a term used to describe those associations in which one animal lives within another, using the host (before or after death) as a place of refuge. Although this mode of preservation has been recorded in the literature, its taphonomic implications have virtually been neglected.

A specimen of the erymid lobster *Palaeastacus?* sp. found in the body chamber of a harpoceratid ammonite from the Lower Toarcian Posidonia Shales of Dotternhausen, southern Germany, is described and illustrated herein. In addition, three specimens of the lobster *Eryma dutertrei* Sauvage, 1891, preserved in the body chambers of large perisphinctid ammonites are recorded from the Portland Limestone Formation (Portlandian) of southern England. The poor record of inquiline preservation of organisms in ammonite body chambers is probably due to the fact that they have not received enough attention rather than because they are rare. The occurrence of ammonite inquilinism in the Posidonia Shales of southern Germany is incompatible with a stagnant basin model, but agrees well with Seilacher's (1990, pp. 123, 126–128) modified model: euxinic stagnant water conditions for most of the time, episodically interrupted by turbidity currents caused by storms. Whereas benthic life was impossible for most organisms during times of stagnant conditions, episodic storm-events brought oxygen down to the sea-floor and made life possible for some months or so. A co-evolutionary relationship between ammonites and the inhabitants of their empty shells is postulated.

## AMMONITE BODY CHAMBER CONTENTS

In comparison with many studies of ammonite taphonomy (e.g. Roll 1935; Lehmann 1976; Seilacher *et al.* 1976; Brenner and Seilacher 1978; Seilacher 1982a, 1982b; Tanabe *et al.* 1984; Maeda 1987, 1991; Neugebauer and Hudson 1987), few studies have dealt with the contents of body chambers. Three types of preservation have been distinguished so far.

(1) Ernst (1967) and Maeda (1991) record post-mortem accumulations of echinoids and small ammonite shells transported into large ammonites.

(2) The preservation of *in situ* ammonite remains. Fossil jaws preserved *in situ* in diagenetically compressed ammonites have been reported (e.g. Lehmann 1976; Morton 1981; Seilacher 1982a; Tanabe *et al.* 1984). Fossil crop/stomach remains of ammonites are rare in most deposits and

preserved only in especially favourable environments. Nixon (1988, p. 650) lists only four examples of *in situ* crop/stomach remains in Jurassic ammonites. Riegraf *et al.* (1984, pl. 1, fig. 7) found nearly twenty specimens with crop and/or stomach remains in the Lower Toarcian Posidonia Shales of south west Germany. Recent finds of several compressed harpoceratid ammonites with preserved crop/stomach contents in the Toarcian black shales of southern Germany provide new data on their diet (Jäger 1991; Jäger and Fraaye work in progress). These new observations confirm the convictions of Nixon (1988) and Tshudy *et al.* (1989) that some, if not all, ammonites were potential predators and/or scavengers of decapod crustaceans.

(3) Inquiline preservation. The fossil record of marine Jurassic sediments indicates that enormous numbers of empty ammonite conchs littered former sea floors. These ammonites supplied food for (nekto)benthic scavengers. There is an extensive literature on shell fracturing tentatively ascribed to crustaceans (Boucot 1990, p. 168). Examples of fractures of Jurassic ammonites presumed to have been produced by decapod crustaceans were recorded by, amongst others, Roll (1935), Seilacher and Wiesenauer (1978), Riegraf *et al.* (1984) and Jäger (1991). Lehmann (1976, p. 135) illustrated the lobster *Eryon* breaking up an ammonite conch with its chelae in search of soft parts. Amongst the favourite prey animals of recent and fossil cephalopods are decapod crustaceans (Nixon 1988; Jäger and Fraaye work in progress). Empty ammonite shells have the potential to shelter the small (nekto)benthic animals common on the soft Jurassic sea floors, and as such Jurassic decapod crustaceans may have been, at least in part, dependent on ammonites for food and shelter.

A review of the literature illustrates many examples of inquiline preservation. A fine example is that of Stewart (1990), who recorded several fish genera found preserved in Upper Cretaceous inoceramid bivalves. An example of probably inhabitation of a Cenomanian crab (*Diaulax oweni* Bell *in* Dixon, 1850) with an ammonite was mentioned by Wright and Collins (1972, pl. 10, figs. 1a–b). Unfortunately, the preparation of the crab has destroyed the *in situ* preservation (J. S. H. Collins, pers. comm.). A second example of a decapod crustacean preserved inside an ammonite body chamber was recorded from the Upper Cretaceous Chalk of northern Germany by Ernst (1967). A concretion containing a body chamber of a scaphitid ammonite filled with faecal pellets illustrated by Bishop (1981, p. 390, fig. K) is another example of Cretaceous ammonite inquilinism.

The first example of ammonite inquilinism from the Jurassic was recorded by Krause (1891, pl. 12, figs 1–2), who described a very well-preserved lobster within a large ammonite of the genus *Gravesia* from the Upper Jurassic (Tithonian) of Germany.

Another example of Jurassic ammonite inhabitation was described briefly by Jäger (1990) from the Toarcian Posidonia Shales of Dotternhausen, southern Germany. Inside two compressed body chambers of harpoceratid ammonites fishes assignable to *Pholidophorus* were found.

A further four specimens illustrating Jurassic ammonite inquilinism by decapod crustaceans, in three different types of preservation are described below.

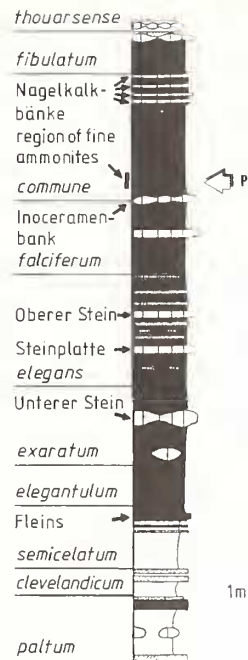
## AMMONITE INQUILINISM IN THE LOWER TOARCIAN POSIDONIA SHALE

### *Geological setting*

The bituminous Lower Toarcian Posidonia Shale is well-known for the excellent preservation of marine reptile, fish and crinoid skeletons found within it (Hauff and Hauff 1981). The facies is widespread not only in southern Germany, but also in northern Germany, England, France and Luxemburg (see map in Riegraf *et al.* 1984, p. 26). In Dotternhausen near Balingen, 70 km south-south-west of Stuttgart and 70 km south-west of Holzmaden, the Posidonia Shale (which is around 9 m thick here) is quarried by the Rohrbach Zement factory to produce cement. In Dotternhausen, the range of fossil species and kinds of preservation is nearly the same as at Holzmaden.

The Posidonia Shale is a bituminous shale, compressed to around 5 per cent. of its original thickness, although limestone layers and concretions display little or no compression. The high content of pyrite and of organic hydrocarbon, the fine lamination of the sediment and the poverty of autochthonous benthos are strong arguments for stagnant water conditions during deposition of

TEXT-FIG. 1. Stratigraphical profile, biostratigraphy and lithostratigraphical marker horizons of the Lower Toarcian of Dotternhausen (after Riegraf 1985, text-fig. 4), with the stratigraphical position of *Palaeastacus?* sp. (RZC 0062).



the Posidonia Shale. From the uppermost part of the Semicelatum Subzone till the lower half of the Fibulatum Subzone, benthic life was totally or nearly totally absent in most horizons, although an impoverished fauna is found in several horizons (Riegraf *et al.* 1984). The layers around the 'Inoceramenbank' at the boundary of the Falciferum/Commune Subzone, represent such horizons with a very impoverished, but not totally absent benthic fauna; some foraminiferan and ostracod species are present (Riegraf 1985, p. 45, fig. 22).

In many layers of the Posidonia Shale, epizoans (mostly serpulids and oysters) often are fixed to the ammonite shells and, as the shell is compressed, the epizoans on the opposite side are also visible being distinctly pressed into the periostracum (Seilacher 1982a). From such specimens Kauffman (1978) developed his 'benthic island' model but, according to the results of Riegraf *et al.* (1984), Riegraf (1985) and Seilacher (1990), these findings seem to represent 'islands in time' (periods of sufficient oxygen content at the sea-floor) rather than islands in space.

Many details of ammonite preservation in the Posidonia Shale have been published by Seilacher *et al.* (1976) and Riegraf *et al.* (1984, p. 52). Usually, the phragmocone is compressed to a paper-thin layer, the living chamber often compressed to a thickness of 1–2 mm. The calcareous shell layers are normally dissolved (this is the reason why septa are visible in few specimens only), but the periostracum is beautifully preserved as a golden brown leaf. Some shells are broken into disarticulated pieces (probably by the action of decapods or fish), but in most specimens the whole periostracum is preserved (though often with cracks, formed during compression) including the delicate rostrum of the apertures of *Harpoceras* and *Hildoceras*.

The excellent preservation of many fossils points to rather low water energy, though current-alignment was recognized by Brenner and Seilacher (1978). The siphuncle is often preserved as a whitish band, and in an estimated 25 per cent. of *Harpoceras* and *Hildoceras* specimens' apychi are still present in the living chamber. Preservation of presumed crop and/or stomach contents is not uncommon (Riegraf *et al.* 1984; Jäger and Fraaye, new data).

Ammonites are present in every horizon of the 9 metre thick Posidonia Shale facies in Dotternhausen. In a section a few decimetres thick in the lowermost part of the Commune Subzone,

between the 'Inoceramenbank' and the 'Nagelkalkbanke' (Text-fig. 1), complete specimens are relatively easy to extract because of the fissility of the shale. Thus in this part of the section ammonites are intensively sampled. Ammonite taxa present (from most to less frequent) are *Dactyloceras commune*, *Harpoceras falciferum* (diameter of adult macroconchs normally 200–300 mm), *Hiodoceras* ex gr. *douvillei/sublevisioni*, *Phylloceras heterophyllum*, *Phymatoceras* cf. *escheri*.

### Material

Decapod crustaceans are rare in the Posidonia Shale except for chelae (propodus plus dactylus) of the swimmer *Uncina posidoniae* Quenstedt 1850 in the 'Fleins' layer and remains of *Coleia?* sp. in the living chamber of ammonites (Jäger and Fraaye, new data) in the lower part of the Commune Subzone. Other remains of decapod crustaceans are rare in the Posidonia Shale of southern Germany, but are found in several horizons. They were described by Beurlen (1928, 1930, 1944), Kuhn (1952) and Hauff and Hauff (1981) and include well-preserved, complete specimens of *Uncina posidoniae*, eight species of *Proeryon*, two *Coleia* species, one *Glyphea*, one *Palaeopagurus* (as *Erymastacus?*), one stomatopode? and one macrure. It is not clear yet how *Proeryon*, which according to its dorsoventrally compressed shape is a typical bottom-dweller, could have managed to live during anoxic conditions, although it may have lived upon floating trunks or have been washed in, although one would expect poorer preservation.

A new specimen (Rohrbach Zement Collection no. 0062) illustrated in Text-figures 2–4 has been determined as *Palaeastacus?* sp. (R. Förster, pers. comm.). According to Förster (1966, p. 126) *Palaeastacus* Bell in Dixon, 1850 is a genus of the family Erymidae. The stratigraphically lowest examples of isolated chelae of *Palaeastacus* are from the lower Sinemurian, while remains of the carapace and more or less complete specimens range from the Upper Jurassic to the Upper Cretaceous.

The new specimen is lying inside the anterior half of the body chamber of an adult macroconch of *Harpoceras falciferum* (Text-fig. 2). The ammonite shell diameter is approximately 270 mm. Though the living chamber is compressed to 1 mm, it is obvious that the crustacean really lies inside the ammonite shell, not at a level above or below. The aptychi are missing. Remains of the siphuncle are preserved. On the ammonite shell at least five oysters (oy.) and four serpulids (serp.) are fixed, probably on both sides of the ammonite, but this is not quite clear. The anterior part of the crustacean is directed towards the aperture of the ammonite, the chelae lying at least 40 mm behind the aperture (which is not preserved). The telson is directed towards the phragmocone. Around the crustacean, and nearly filling the ammonite body chamber, are areas which seem to be composed of masses of elliptical to subspherical bodies. These have an approximate maximum diameter of 1.5–2.0 mm, are compressed and indistinct, and are here interpreted as crustacean coprolites.

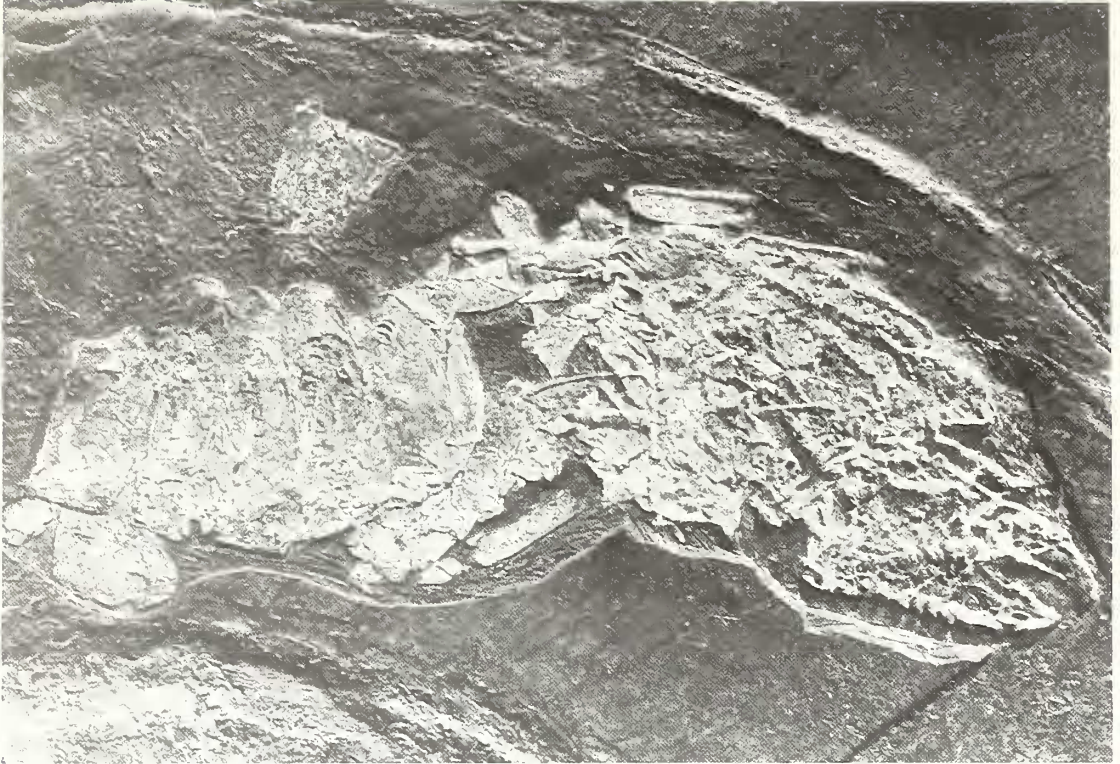
Although the *Palaeastacus?* is almost complete (remains of the chelae, feet, abdomen and telson are visible) and the parts of the skeleton are lying close together, the disarticulation and compression of the skeletal parts makes proper description difficult. The anterior half of the decapod seems to be composed of two chelipeds and a few other fragments, most of them probably fragments of thoracopods. Nothing distinct is visible of the carapace which perhaps is lying underneath the chelipeds ('underneath' is applied according to the present state of the shale slab).

The slab was not found *in situ*, and it is therefore unknown which is the upper and which the lower surface. In both chelipids, dactylus (d), propodus (p) and carpus (c) are lying close together, with only minute traces of disarticulation. One merus (m) is present. The two chelae are lying nearly parallel to each other and close together, with the dactyli touching each other. The chelae are covered with very strong spines, especially at the border. The carpi are triangular and spiny, but the spines are not quite as strong as in the propodi. The meri of the chelipeds are not properly distinguished from the leg fragments (l). Only one slender rectangular remnant seems to be a merus, but it is not clear to which of the chelipeds it belongs. Between the anterior and the posterior half of the crustacean there is an area, approximately 15 mm long, where only few skeletal remains are



TEXT-FIG. 2. *Palaeastacus?* sp. RZC 0062; preserved in body chamber of *Harpoceras falciferum*; large areas with elliptical coprolites indicated with black arrows; Posidonia Shales, Lower Toarcian; Dotternhausen, Germany;  $\times 0.88$ .

preserved. In the abdomen, five (or perhaps six) of the somites (s) are articulated to each other and clearly visible (Text-fig. 3). Together they are nearly 50 mm long. The telson is disarticulated from the abdomen. After 25 mm of free space, only one large plate of the telson (t) can be identified.



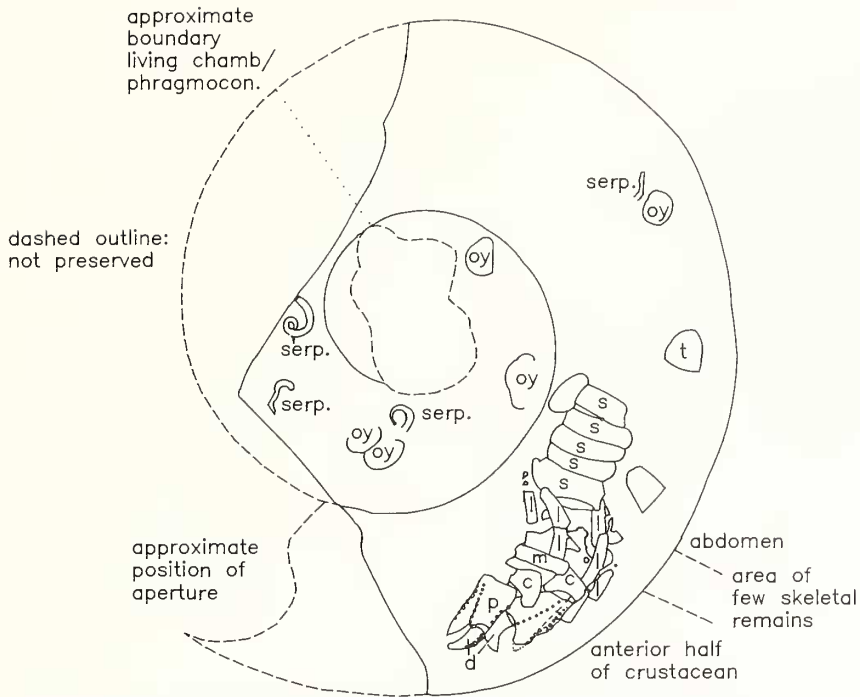
TEXT-FIG. 3. *Palaeastacus?* sp. RZC 0062; preserved in body chamber of *Harpoceras falciferum*, showing details of the spiny chelae and the abdomen; Posidonia Shales, Lower Toarcian; Dotternhausen, Germany;  $\times 1.5$ .

#### *Ecological interpretation*

According to Förster (1966, p. 153) Erymidae preferred muddy soft-bottoms in relatively shallow water near the coast. They probably dug themselves into the mud or hid under stones for resting, for moulting or for protection. Erymidae were probably carnivorous or carrion feeders. Perhaps the fractures in ammonite body chambers, which sometimes look as if they were made by a 'tin-opener' (Riegraf *et al.* 1984, p. 58, fig. 15; Jäger 1991, figs 3–4), were made by the strong chelae of *Palaeastacus?*. However, *Palaeastacus?* is too rare to have been responsible for all such ammonite destruction.

The *Palaeastacus?* is too large and too complete to be the crop and/or stomach contents of the ammonite (as are many specimens of small and disarticulated *Coleia?* sp. to be described in a later paper (Jäger and Fraaye, new data), their interpretation as a moulted skeleton in Jäger (1991, p. 33) probably being wrong). On the other hand the crustacean was not large enough to be able to walk around while within the ammonite shell in the manner of a hermit crab, which, moreover, would have a less calcified abdomen.

Though the skeleton of *Palaeastacus?* should have been sheltered inside the ammonite shell against destruction, disarticulation is more distinct than in specimens found loosely in the sediment. This was the main reason why Jäger (1991, p. 33) interpreted the *Palaeastacus?* as a moult. In fossil crustaceans, moulted skeletons are often recognizable by the splitting of the carapace and by an approximate right angle between the longitudinal axes of the carapace and the abdomen (Förster 1966, p. 154). In the *Palaeastacus?*, however, the carapace is poorly visible, and the right angle may be due to compression. Thus, it cannot be decided if it is a moult or a dead crustacean. The area



TEXT-FIG. 4. *Palaeastacus?* sp. RZC 0062; preserved in body chamber of *Harpoceras falciferum*; outline of skeletal elements partly idealized, because some of the outlines are hardly visible in the original; for explanation of abbreviations see text; Posidonia Shales, Lower Toarcian; Dotternhausen, Germany;  $\times 0.33$ .

with only few skeletal remains between the anterior half and the abdomen is an argument for breakage between carapace and abdomen during moulting.

Interpreting the small spherical structures as decapod coprolites, the animal must have lived for a relatively long time inside the body chamber (Text-fig. 4). This means that anoxic conditions at the sea-floor must have been interrupted for this period.

#### AMMONITE INQUILINISM IN THE PORTLAND LIMESTONE FORMATION

##### *Geological setting*

The Isle of Portland is a natural peninsula about 6 km long, near Weymouth, on the southern coast of England. The specimens described below were collected in the ARC Broadcraft Quarry, north-east of the village of Easton during a one-week field trip in March 1990.

The Portland Group consists of a lower Portland Sand Formation and an upper Portland Limestone Formation. The Portland Sand Formation grades down into the black shale sequence of the Kimmeridge Clay. The Portland Limestone Formation is overlain by evaporitic limestone-marl sequence known as the Purbeck Group. The Portland Group represents a regressive sequence (Townson 1975). The Portland Sand Formation consists mainly of clay-, silt- and sandstones, accumulated in a marine environment below wave base. The Portland Limestone Formation starts with a 3 m thick Basal Shell Bed. This bed contains a rich biota of mainly bivalves, gastropods and serpulids. The upper 25 m of the Portland Limestone Formation consists of cherty limestones deposited in an open shelf environment that pass up into shallow-water cross-bedded oolitic grainstones.

Some levels within the cherty part of the Portland Limestone Formation are rich in large perisphinctid ammonites whose diameter often exceeds 0.5 m. The grainstones yield numerous

oncolitic algae, bivalves and gastropods. The lower Purbeck Group finally grades through stromatolitic levels with silicified tree trunks into fossil soils and lagoonal limestones.

Two specimens described below were collected from the lower part (*Galbanites* (*Kerberites*) *kerberus* Zone) of the Portland Limestone Formation. The environment was thought by Townson (1975) to have been moderately deep and tranquil marine. A third specimen (Collection Geo Centrum Brabant, no. MAB k. 0049) of a *Glaucolithites* sp. with two partially preserved chelae of *Eryma* sp. coincident with the body chamber was discovered in the Portland Clay Member, a few metres below the Basal Shell Bed, forming the topmost Portland Sand Formation (*Glaucolithites glaucolithus* Zone).

### Material

The first specimen (Collection Geo Centrum Brabant, no. MAB K0047) was found in a fragment of an ammonite body chamber 250 mm maximum length, 150 mm maximum width. The preservation of the segments of the lobster is very good. There are no signs of post-mortem transport and only a few compactional cracks are present. The axis of the lobster body runs parallel with the ammonite coiling (Text-figs 5–6). The lobster is embedded within an elongate concretion of slightly banded, light grey chert. This concretion in its turn runs parallel with the outline of the body chamber.

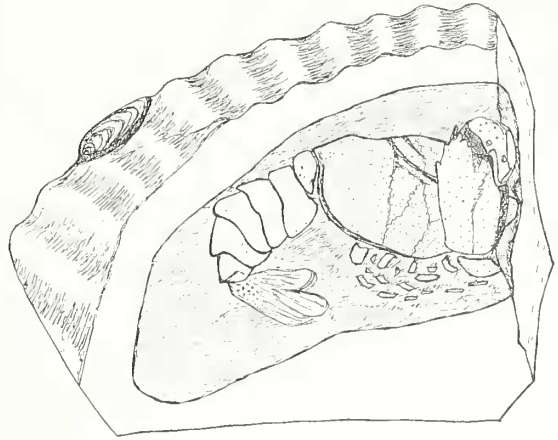
Observations and experimental data from modern marine environments, and from the common Holocene subfossil decapods from concretions along the coasts of south-eastern Asia and northern



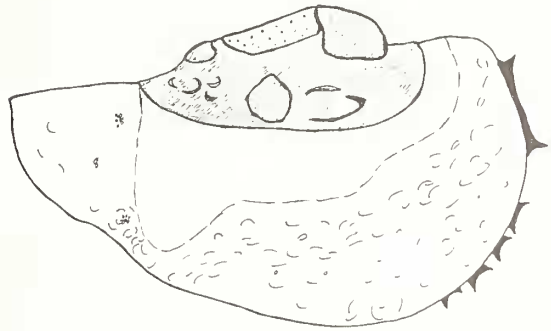
TEXT-FIG. 5. *Eryma dutertrei* Sauvage. MAB K0047; embedded within chert concretion in perisphinctid ammonite body chamber; Portland Limestone Formation, Portlandian; Broadcraft Quarry, Portland, England;  $\times 0.8$ .



TEXT-FIG. 6. *Eryma dutertrei* Sauvage. MAB K0047; schematic sketch showing chert concretion and preservation of decapod segments in perisphinctid ammonite body chamber; Portland Limestone Formation, Portlandian; Broadcraft Quarry, Portland, England;  $\times 0.5$ .



TEXT-FIG. 7. *Eryma dutertrei* Sauvage. MAB K0047; schematic sketch of cross section of perisphinctid body chamber, showing position of chert concretion, bioclasts and epibionts; Portland Limestone Formation, Portlandian; Broadcraft Quarry, Portland, England;  $\times 0.5$ .



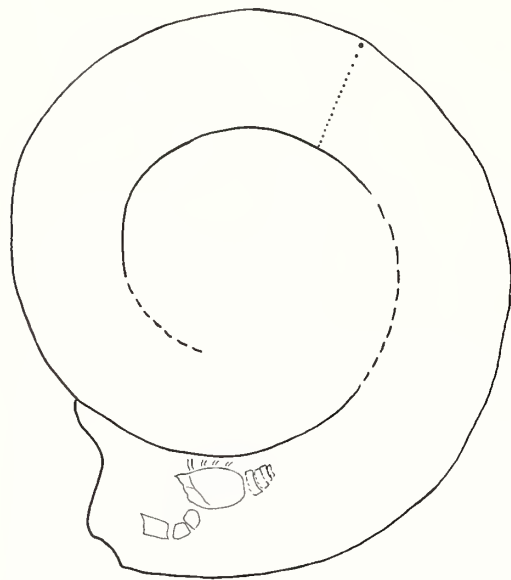
Australia indicate that concretions may form very rapidly around decaying decapod crustaceans (Schäfer 1951; Moore 1969; Plotnick 1986). The process involves locally increased pH, a result of ammonia produced during organic decomposition, and bacterial sulphate reduction. In relatively pure, fine-grained carbonate rocks, chert nodules may develop in or around fossils or burrows, suggesting a possible association with organic micro-environments. The aggregation of silica into nodules apparently takes place during recrystallization of biogenic silica (often sponge spicules). Articulated skeletal remains indicate that the formation of chert concretions was associated with anaerobic decay of organic matter immediately following burial. The field and laboratory studies of Schäfer (1951) and Plotnick (1986) indicate that the decay of soft tissues and the reduction in cuticle rigidity led to the loss of physical integrity of decapod specimens between a few weeks and several months. Size and shape of concretions are strongly influenced by the type of organic remains they grow in or around (Bishop 1981).

The large carapace is covered with fine granules, the density of which decreases towards the rostrum. Unfortunately, most of the cephalic portion is covered by the right cheliped obscuring the cervical, gastro-orbital and hepatic regions. The characteristic intestinal margin is well-preserved. The long branchiocardiac and short postcervical grooves run parallel and are slightly disturbed by compressional cracks. Of the right chela, only the ischium, merus and proximal part of the carpus are visible. The chela is covered with very coarse granules; their density decreases laterally. Some large tubercles appear on the lateral part of the merus and proximal part of the carpus. The long finely granulated and denticulate movable and fixed fingers of both chelipeds are equal in size. Other thoracopods are only partially visible in the chert concretion. The abdomen consists of four more or less equal-sized somites between the considerably smaller first and sixth somites. The posterior margin of each somite overlaps the anterior margin of the adjacent one. The somites are covered with coarsely spaced granules and some tubercles. The tuberculation increases in strength

posteriorly and extends to the telson. The relatively long uropods are faintly striated. The few preserved cuticle fragments show tubercles of various sizes.

The ammonite has only part of its body chamber preserved as a composite mould on which several oysters are attached. The size of the epibiont oysters increases towards the venter of the ammonite (Text-fig. 7). Its body chamber is filled with a bioclastic wackestone, the majority of the bioclasts being small bivalves and serpulids. The body chamber contains the lobster described preserved within a chert concretion.

The second specimen (Collection Geo Centrum Brabant, no. MAB K0048) was found in an almost complete perisphinctid ammonite 380 mm in diameter. The incomplete carapace of the crustacean is split along the dorsal midline. Only the right chela and a few disassociated segments of the abdomen and pereopods are present (Text-fig. 8). The same displacement and splitting of the



TEXT-FIG. 8. *Eryma dutertrei* Sauvage. MAB K0048; schematic sketch showing molting remains in ammonite body chamber; Portland Limestone Formation, Portlandian; Broadcraft Quarry, Portland, England;  $\times 1$ .

carapace are seen for example, in the Jurassic *Glyphea* and the Cretaceous *Hoploparia* and *Onopareia* and are recognized as indicative of a moulting position. The gastric and antennal regions of the carapace are missing because it was fractured along the cervical groove. The branchiocardiac, postcervical and inferior grooves are distinct and match the description of *Eryma dutertrei* Sauvage, 1891 in Förster's (1966, p. 117) revision of the erymids.

Except for the chert concretion, the infilling of the ammonite body chamber is the same as specimen MAB k0047 except that in this case several little gastropods and some plant remains are also present. The intense upper-side erosion and covering with oysters and other bivalves show that the ammonite acted as a benthic 'island' for a relatively long time.

## DISCUSSION

If ammonite inquilinism was a common feature, bite traces on ammonite shells produced by, for example, sharks and reptiles are not necessarily the result of hunting on living ammonites. It is possible that these predators may have hunted the animals which lived, hid or moulted within empty ammonite conchs. By grabbing and shaking, the predators could have forced these inhabitants out of their refuge.

Several groups of organisms develop extreme adaptations to specialized habitats (Boucot 1990). It is likely that, in addition to decapod crustaceans, other (nekto)benthic groups (e.g. fishes, dwarf

ammonites) adapted an ammonite inquiline mode of life, simply because on offshore fine-grained Mesozoic sea floors there were no other suitable hiding places. We therefore concur with Ernst (1967) and Matsumoto and Nihongi (1979), who respectively explained certain accumulations of thin shelled echinoids and small heteromorph ammonites in larger ammonites as *in situ* cave dwellers. Some examples of post-mortem accumulations recorded by Maeda (1991) could also have been ammonite inhabitants. Post-mortem drift is not consistent with the fact that in the same sediments the jaw apparatus of the ammonites are comparatively often preserved within the body chambers (Hirano 1991). Maeda (1991) also recorded considerable amounts of plant remains, disarticulated crinoid stalks and inoceramid shells to have accumulated in body chambers of large ammonites. Lehmann (1975), Lehmann and Weischat (1973) and Riegraf *et al.* (1984) noted accumulations of crinoid ossicles and inoceramid shells within Jurassic ammonites.

There are several modern examples of crustaceans which store pieces of animal material and seagrass leaves in their burrows as bacterial horticultures (Bromley 1990). Were ammonites ideal dining rooms for decapod crustaceans or did the decapods have their own horticultures, or both? And were these horticultures plundered by other (nekto)benthic animals such as fishes and echinoids? Whatever may be the case, the accumulation of organic matter within the ammonite shells certainly increased the preservational potential of the ammonites.

*Acknowledgements.* We thank Mr J. S. H. Collins, Dr M. Nixon and Professor G. Westermann for their helpful suggestions and Mr Poole from ARC Aggregates for assistance in the field. We also thank Mr G. Rohrbach the director and Mr F. Klein the manager, of Rohrbach Cement, who support collection, preparation and research of fossils. Thanks are also extended to A. van den Engel and A. Robbmond for their help in the field and to J. Jagt and W. Fraaye for their comments and suggestions for improving this paper.

#### REFERENCES

- ALDINGER, H. 1965. Zur Ökologie und Stratinomie der Fische des Posidonienschiefers (Lias epsilon). *Senckenbergiana Lethaea*, **46a**, 1–12.
- BEURLEN, K. 1928. Die Decapoden des Schwäbischen Jura mit Ausnahme der aus den oberjurassischen Plattenkalk stammenden. *Palaeontographica, Abteilung A*, **70**, 115–282.
- 1930. Nachträge zur Decapodenfauna des Schwäbischen Jura. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B, Beilagen-Band*, **64**, 219–234.
- 1940. Neue Reste von *Proeryon* (Crustacea, Decapoda, Eryonidae). *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B, Beilagen-Band*, **88**, 374–384.
- BISHOP, G. A. 1981. Occurrence and fossilization of the *Dakoticander* Assemblage, Upper Cretaceous Pierre shale, South Dakota. 383–413. In GRAY, J., BOUCOT, A. J. and BERRY, W. B. N. (eds). *Communities of the past*. Hutchinson Ross, Stroudsburg, 530 pp.
- BOUCOT, A. J. 1990. *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam, 725 pp.
- BRENNER, K. and SEILACHER, A. 1978. New aspects about the origin of the Toarcian Posidonia Shales. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **157**, 11–18.
- BROMLEY, R. G. 1990. *Trace fossils: biology and taphonomy*. Unwin Hyman Ltd., London, 280 pp.
- DIXON, F. 1850. *The geology and fossils of the Tertiary and Cretaceous formations of Sussex*. London, 422 pp.
- ERNST, G. 1967. Über Fossilnester in *Pachydiscus* – Gehäusen und das Lagenvorkommen von Echiniden in der Oberkreide NW-Deutschlands. *Paläontologische Zeitschrift*, **41**, 211–229.
- FÖRSTER, R. 1966. Über die Erymiden, eine alte konservative Familie der mesozoischen Dekapoden. *Palaeontographica, Abteilung A*, **125**, 61–175.
- HAUFF, B. and HAUFF, R. B. 1981. *Das Holzmadenbuch*. Holzmaden, 136 pp.
- HIRANO, H. 1991. Phyletic evolution of desmoceratine ammonoids through OAE at C/T boundary. 14–15. In *The Ammonoidea: evolution and environmental change. Programme with abstracts*. The Systematics Association, London, 80 pp.
- HOUSE, M. 1989. *Geology of the Dorset Coast*. Geologists' Association, London, 162 pp.
- JÄGER, M. 1990. Lias epsilon von Dotternhausen. *Fossilien*, **7**, 274–277.
- 1991. Lias epsilon von Dotternhausen. *Fossilien*, **8**, 33–36.
- KAUFFMAN, E. G. 1978. Benthic environments and paleoecology of the Posidonienschiefer (Toarcien). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **157**, 18–36.

- KRAUSE, P. G. 1891. Die Decapoda des norddeutschen Jura. *Zeitschrift der Deutschen geologischen Gesellschaft*, **43**, 171–225.
- KUHN, O. 1952. Neue Crustacea Decapoda und Insecta aus dem untersten Lias epsilon von Nordfranken. *Palaeontographica, Abteilung A*, **101**, 153–166.
- LEHMANN, U. 1975. Über Nahrung und Ernährungsweise von Ammoniten. *Paläontologische Zeitschrift* **49**, 187–195.
- 1976. *Ammoniten: Ihr Leben und ihre Umwelt*. Enke Verlag, Stuttgart, 171 pp.
- 1979. The jaws and radula of the Jurassic ammonite *Dactyloceras*. *Palaeontology*, **22**, 265–271.
- and WEISCHAT, W. 1973. Zur Anatomie und Ökologie von Ammoniten. Funde von Kropf und Kiemen. *Paläontologische Zeitschrift*, **47**, 69–76.
- MAEDA, H. 1987. Taphonomy of ammonites from the Cretaceous Yezo Group in the Tappu area, northwestern Hokkaido, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **148**, 285–305.
- 1991. Sheltered preservation: a peculiar mode of ammonite occurrence in the Cretaceous Yezo Group, Hokkaido, north Japan. *Lethaia*, **24**, 69–82.
- MATSUMOTO, T. and NIHONGI, M. 1979. An interesting mode of occurrence of *Polyptychoceras* (Cretaceous heteromorph ammonoid). *Proceedings of the Japan Academy*, **55B**, 115–119.
- MOORE, R. C. (ed.) 1969. *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 651 pp.
- MORTON, N. 1981. Aptychi: the myth of the ammonite operculum. *Lethaia*, **14**, 57–61.
- NEUGEBAUER, J. and HUDSON, J. D. 1978. Neuere Untersuchungen zur Ammonitenerhaltung. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **157**, 188–193.
- NIXON, M. 1988. The feeding mechanism and diets of Cephalopods – living and fossil. 641–652. In WIEDMANN, J. and KULLMANN, J. (eds). *Cephalopods – present and past*. Schweizerbart, Stuttgart, 725 pp.
- PLOTNICK, R. E. 1986. Taphonomy of a modern shrimp: implications for the arthropod fossil record. *Palaeo*, **1**, 286–293.
- QUENSTEDT, F. 1850. Über *Mecochirus* im braunen Jura bei Gammelshausen und einige andere Krebse. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg*, **6**, 186–197.
- RIEGRAF, W. 1985. Mikrofauna, Biostratigraphie und Fazies im Unteren Toarcium Südwestdeutschlands und Vergleiche mit benachbarten Gebieten. *Tübinger Mikropaläontologische Mitteilungen*, **3**, 1–233.
- WERNER, G. and LÖRNER, F. 1984. *Der Posidonienschiefer – Biostratigraphie, Fauna und Fazies des südwestdeutschen Untertoarciums (Lias epsilon)*. Enke, Stuttgart, 195 pp.
- ROLL, A. 1935. Über Frassspuren an Ammonitenschalen. *Zentralblatt für Mineralogie, Geologie und Paläontologie, B*, **1935**, 120–124.
- SAUVAGE, H. 1891. Note sur les Crustacés des terrains jurassiques supérieur du Boulonnais. *Annales des Sciences naturelles Zoologie*, **12**, 83–96.
- SCHÄFER, W. 1951. Fossilisations-Bedingungen brachyurer Krebse. *Senckenbergische Naturforschungs Gesellschaft, Abhandlungen*, **485**, 221–238.
- SEILACHER, A. 1982a. Ammonite shells as habitats in the Posidonia Shales of Holzmaden – floats or benthic islands? *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1982**, 98–114.
- 1982b. Posidonia Shales (Toarcian, S. Germany) – stagnant basin model revalidated. 24–55. In GALLITELLI, E. M. (ed.). *Palaeontology, essential of historical geology*. Modena Press, Venice, 298 pp.
- 1990. Die Holzmadener Posidonienschiefer – Entstehung der Fossilagerstätte und eines Erdölmuttergesteins. 107–131. In WEIDERT, W. K. (ed.) *Klassische Fundstellen der Paläontologie*, **2**, Goldschneck, Korb, 265 pp.
- ANDALIB, F., DIETL, G. and GOCHT, H. 1976. Preservational history of compressed Jurassic ammonites from southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **152**, 307–356.
- and WIESENAUER, E. 1978. Preservational and adaptional history of belemnites. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **157**, 145–149.
- STEWART, J. D. 1990. Preliminary account of halecostome-inoceramid commensalism in the Upper Cretaceous of Kansas. 51–57. In BOUCOT, A. J. (ed.). *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam, 725 pp.
- TANABE, K., INAZUMI, A., TAMAHAMA, K. and KATSUTA, T. 1984. Taphonomy of half and compressed ammonites from the Lower Jurassic black shales of the Toyora area, west Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **47**, 329–346.
- TOWNSON, W. G. 1975. Lithostratigraphy and deposition of the type Portlandian. *Journal of the Geological Society of London*, **131**, 619–638.

- TSHUDY, D. M., FELDMANN, R. M. and WARD, P. D. 1989. Cephalopods: biasing agents in the preservation of lobsters. *Journal of Paleontology*, **63**, 621–626.
- WRIGHT, C. W. and COLLINS, J. S. H. 1972. British Cretaceous Crabs. *Monograph of the Palaeontographical Society*, **126**, 1–114.

RENÉ FRAAYE

Geo Centrum Brabant  
St. Lambertusweg 4  
5291 NB Boxtel  
The Netherlands

MANFRED JÄGER

Rohrbach Zement  
D-7466 Dotternhausen  
Germany

Typescript received 24 February 1993

Revised typescript received 20 November 1993